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RESEARCH ARTICLE

Kloss Gibbon (*Hylobates klossii*) Behavior Facilitates the Avoidance of Human Predation in the Peleonan Forest, Siberut Island, Indonesia

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Kloss gibbons (*Hylobates klossii*) are endemic to the Mentawai Islands in Indonesia and have been subject to human predation for more than 2000 years in the absence of any other significant predators. We investigate the behavior of Kloss gibbons that may be attributed to avoiding human predation. We observed Kloss gibbons in the Peleonan forest in the north of Siberut Island, the northernmost of the Mentawai island chain, over 18 months in 2007 and 2008, and collected data on their singing behavior, the number of individuals present during different conditions and their responses to humans. We examine behaviors that may reduce the risk of predation by humans during singing (the most conspicuous gibbon behavior), daily non-singing activities and encounters with humans. The individual risk of being stalked by hunters is reduced by singing in same-sex choruses and the risk of successful capture by hunters during singing is reduced by singing less often during daylight hours and by leaving the location of male pre-dawn singing before full light (reducing the visual signal to hunters). Groups in the Peleonan also fission during non-singing daily activity and rarely engage in play or grooming, enhancing the crypticity of their monochromatic black pelage in the canopy. We also observed a coordinated response to the presence of humans, wherein one adult individual acted as a "decoy" by approaching and distracting human observers, while other group members fled silently in multiple directions. "Decoy" behavior occurred on 31% of 96 encounters with unhabituated Kloss gibbons that detected our presence. "Decoy" individuals may put themselves at risk to increase the survival of related immatures (and adult females with infants) who have a greater risk of predation. We argue that, in combination, these behaviors are an evolved response to a long history of predation by humans. Am. J. Primatol. 77:296–308, 2015. © 2014 Wiley Periodicals, Inc.

Key words: ***Hylobates klossii*; anti-predator behavior; predation; human hunting; crypsis**

INTRODUCTION

Predation plays a significant role in the evolution of primate social systems and behavior [Isbell, 1994; Stanford, 2002; van Schaik, 1983]. The act of predation can be divided into three phases: search, pursuit, and handling [Colquhoun, 2007]. The anti-predation strategies of prey should minimize the success of a predator at each of these three phases [Colquhoun, 2007]. While the cryptic nature of most predators of primates makes direct sightings of predator-prey interactions rare [Enstam, 2007; Fichtel, 2012; Isbell, 1994; Morino, 2010], the reactions of primates to humans can be observed directly. Humans pose a threat to most primate species due to the hunting pressure they impose [Fichtel, 2012; Isbell, 1994; Peres, 1990; Zapata-Ríos et al., 2009], but, despite the strong selective pressure of long-term human predation experienced by multiple primate species, human predation is rarely included in analyses of anti-predator behavior [Fuentes & Hockings, 2010; Papworth et al., 2013]. Kloss gibbons (*Hylobates klossii*) have been subject to human predation for over 2000 years in an area devoid of other diurnal predators and with few large mammal prey species [Tenaza & Tilson, 1985]. Herein we describe the reactions of Kloss gibbons to humans and examine the suite of behaviors exhibited by this species that may be attributed to avoiding human predation. We advance the hypothesis that an array of behavioral traits exhibited by Kloss

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gibbons is the result of selective pressures associated with human predation.

Predation is one of the strongest selective pressures faced by most animal species; failing to avoid predation severely reduces fitness [Lima & Dill, 1990]. All gibbon species, including Kloss gibbons, appear to suffer lower rates of predation than other primate species [Paciulli, 2004; Tenaza & Tilson, 1985; Uhde & Sommer, 2002], but this does not diminish the significance of predation as a selective pressure on this group of primates. Low current predation rates may be a reflection of effective predation avoidance strategies of prey species [Zuberbühler, 2007; Morino, 2010]. In addition, it is predation *risk* not *rate* that propels and maintains current predator avoidance behaviors in prey populations [Hill & Dunbar, 1998]. Prey animals seek to lower their predation risk by reducing their encounter rate with predators and by lowering the chance of a successful attack when encounters occur [Colquhoun, 2007; Stanford, 2002]. Predation risk may vary both geographically and temporally; thus, predator avoidance strategies will vary depending on the predation risk associated with an environment, time of day or even the behavior of a predator itself [Cowlishaw, 1994; Hill & Dunbar, 1998; Lima & Bednekoff, 1999; Miller & Treves, 2007; Papworth et al., 2013].

The impact of even low levels of predation on animals with low reproductive rates is significant [Uhde & Sommer, 2002]. Gibbons have a prolonged juvenile period and individuals may not reproduce until after 8 years of age [Brockelman et al., 1998; Chivers & Raemaekers, 1980]. Additionally, a single wild female may produce as few as five offspring in her lifetime [O'Brien & Kinnaird, 2011; Palombit, 1995; Reichard, 2003; Reichard & Barelli, 2008; Tilson, 1981]. The loss of even one offspring to predation can significantly reduce a female gibbon's inclusive fitness [Uhde & Sommer, 2002]. The cost to male gibbons is also high as males' reproduction is usually limited to that of one female [Brockelman, 2009]. Thus, gibbons should exhibit behaviors that reduce the encounter rate with predators and reduce the risk of successful predation upon encounter. Common anti-predator behaviors in gibbons include: choosing sleeping trees which reduce the risk of predation [Fan & Jiang, 2008; Phoonjampa et al., 2010; Reichard, 1998; Tenaza & Tilson, 1985], alarm calling and vocal signals that relay information about predators to neighboring conspecifics [Clarke et al., 2006; Tenaza & Tilson, 1977] and the harassment of some predators [Kappeler, 1981; Uhde & Sommer, 2002]. Given that other primates display the ability to evolve behavioral responses to human hunters within a few generations [Bshary, 2001; Croes et al., 2007] and that gibbons exhibit behavioral plasticity and the ability to problem solve [Beck, 1967; Cunningham et al., 2006; Geissmann, 2009], we expect to see a suite of behaviors in Kloss gibbons that have evolved in response to 2000 or more years of predation by humans.

Predators of hylobatids include: reticulated pythons (*Python reticulatus*), large felids, such as the clouded leopard (*Neofelis nebulosa*) and tiger (*Panthera tigris corbetti*), some large raptors that pose a threat to immature gibbons, such as the mountain hawk eagle (*Spizaetus nipalensis*) and changeable hawk eagle (*Spizaetus cirrhatus*), and humans (*Homo sapiens*) [Clarke et al., 2012; Kappeler, 1981; Morino, 2010; Tenaza & Tilson, 1985; Uhde & Sommer, 2002]. Felids, raptors and snakes may employ a "sit-and-wait" strategy or stalk and ambush unsuspecting prey [Uhde & Sommer, 2002]. Human hunters rely on stealth to approach prey, but the distance at which hunters can "strike" prey is greater than that of other predators, because they use projectile weapons such as rifles or traditional bow and arrows [Miller & Treves, 2007]. For this reason, gibbons that have suffered human predation pressure may have been selected to respond differently to humans than to other potential predators. In response to circling raptors, gibbons drop down in the canopy and avoid exposed branches and, following the detection of a stationary raptor within the canopy or a python or felid, gibbons may produce alarm calls and harass the predator for more than 10 min [Clarke et al., 2012; Kappeler, 1981; Uhde & Sommer, 2002]. Alarm calls and harassment may deter a predator by signaling discovery [Crofoot, 2012; Curio, 1978; Zuberbühler et al., 1999]. Human hunters, on the other hand, may still capture alert prey if they expose themselves or approach a hunter [Miller & Treves, 2007]. In most species, gibbons will flee in response to humans [Cheyne, 2010; Clarke et al., 2012; Kappeler, 1981]. Likewise, we expect Kloss gibbons to limit their exposure to humans, both by reducing the risk of detection and also by responding in a way which reduces the risk of successful capture.

While most species of gibbons are subject to some human predation [Fan & Huo, 2009; Geissmann, 2007; Geissmann et al., 2009; Phoonjampa & Brockelman, 2008; Qingyong & Xuelong, 2009; Whittaker, 2009], *H. klossii* are the only species for which humans are the primary predator [Tenaza & Tilson, 1985]. Kloss gibbons have been subject to human predation for more than 2000 years [Tenaza, 1976; Tenaza & Tilson, 1977, 1985; Tenaza & Mitchell, 1985]. The Mentawai islands are devoid of large felids and raptors and, as a result, the primates endemic to these islands experienced a relaxation in predation pressure from the time they colonized the islands roughly 500,000 years ago until the arrival of humans 2000–3000 years ago [Batchelor, 1979; Harrison et al., 2006; Loeb, 1935; Tenaza & Tilson, 1985; Tilson, 1980]. Since their arrival, humans have relied on primates as a protein source, due to the paucity of large bodied mammals on the islands

[Tenaza & Tilson, 1985; Whittaker, 2006]. The hunters of the Mentawai Islands are primarily diurnal predators that rely on sound and vision to detect, stalk and kill their prey [Tenaza, 1976; Tenaza & Tilson, 1985]. We expect that Kloss gibbons will minimize visual and aural cues during daily activity to avoid detection by humans and that they will exhibit behaviors that minimize the risk associated with conspicuous activities, such as singing.

Behaviors Minimizing the Risk Associated With Singing

Loud calls of many species are exploited by predators to facilitate locating and pursuing prey [Bshary, 2001; Mougeot & Bretagnolle, 2000; Ryan et al., 1981; Tuttle & Ryan, 1982]. Like all hylobatids, Kloss gibbons sing loud songs that can be heard by humans up to 1 km away and, when females sing, they engage in a visual display of branch-shaking and swift, acrobatic brachiation within the singing tree [Dooley et al., 2013; Tenaza, 1976; Whitten, 1982a]. Thus singing is the most conspicuous Kloss gibbon behavior. In fact, Mentawai hunters orient to singing gibbons then use the volume of the songs to mask the sound of their approach [Tenaza, 1976]. In most hylobatids, mated males and females coordinate their sex-specific songs to produce a duet, Kloss gibbons however, only sing solo songs [Geissmann, 2002]. Both sexes sing in same-sex choruses where their solo songs overlap but are not generally synchronized with the songs of neighboring conspecifics [Dooley et al., 2013; Tenaza, 1976; Whitten, 1982a]. Typically males sing before dawn between 0400 and 0600 hours and females sing in the mid-morning between 0700 and 1000 hours; males occasionally sing after dawn [Dooley et al., 2013; Tenaza, 1976]. Female Kloss gibbons sing less often than other *Hylobates* species [Cowlishaw, 1992]. We examine how the singing behavior of Kloss gibbons minimizes the risk of human predation.

Crypsis

Crypsis is a common strategy for avoiding detection by predators [Kappeler, 1981; Reichard, 1998; Uhde & Sommer, 2002]. Unlike most other gibbon species, Kloss gibbon pelage is monochromatic black without the face rings and pelage variation of other gibbon species [Geissmann, 2003]. For animals with trichromatic vision (such as humans), it is difficult to see dark monochromatic pelage in the low and backlit forest canopy [Sumner & Mollon, 2003]. As a result, Kloss gibbons are well camouflaged in the forest canopy during periods of minimal movement. We expect that, due to a long history of human predation, Kloss gibbons will remain cryptic during non-singing activity and will, therefore, spend little time engaged in behavior that causes canopy displacement or makes them more visible to predators.

Response to Humans

Like other predators, human hunters rely on stealth to successfully hunt gibbons [Tenaza & Tilson, 1985]. When Kloss gibbons detect humans they often emit an alarm call, which is loud enough to alert neighboring groups and may elicit an alarm call in response [Tenaza & Tilson, 1977]. Unlike the modified duet calls given by *Hylobates lar* in response to predators [Clarke et al., 2006], the alarm calls of *H. klossii* are distinct from the male and female songs and Tenaza & Tilson [1977] argue that they evolved via kin selection, as individuals from separate groups are often related [Tenaza & Tilson, 1977]. This behavior effectively reduces immediate predation risk as hunters tend to give up a hunt when gibbons alarm because alert gibbons are difficult to capture and other primate species in the nearby area are also alerted [Tenaza & Tilson, 1977].

In addition to alarm calling by Kloss gibbons following the detection of humans, we also expect to observe behaviors which not only minimize the individual risk of capture by hunters, but also protect other group members because gibbons live in family groups. Individuals at greatest risk of human predation are likely to be females burdened with infants, as they can be slow and clumsy [Anderson, 1986; Miller & Treves, 2007; Reichard, 1998] and, more recently, because infants may be targeted for the pet trade [Whittaker, 2006]. Independent immatures may also be at high risk, not because they are the preference of hunters [their smaller size would logically make them less desirable to hunters looking for meat; Peres, 1990; Zapata-Ríos et al., 2009], but because their inexperience in navigating and negotiating the forest canopy makes them an easier target than more adept adults [Reichard, 1998]. In groups of related primates, adult males are more likely to mob predators, reducing the risk to immatures and females with infants [Anderson, 1986; Arlet & Isbell, 2009; Cheney & Wrangham, 1987; Stanford, 1995; van Schaik & Noordwijk, 1989]. There is some suggestion that male Kloss gibbons may distract humans while other individuals flee [Tenaza, 1974]. Herein we describe the distinctive reactions of Kloss gibbons to us as human observers.

METHODS

Site

This study was conducted at the Siberut Conservation Programme (SCP) field station in the Peleonan forest in the north of Siberut Island, Indonesia (1° 01.031′S, 98°50.166′E, Fig. 1). Over the course of 18 months from June 2007 until December 2008, at least five separate gibbon groups (A, B, C, D, and N) were observed by the primary researcher (HD), a research assistant and four local field guides. The primates within the research area have been

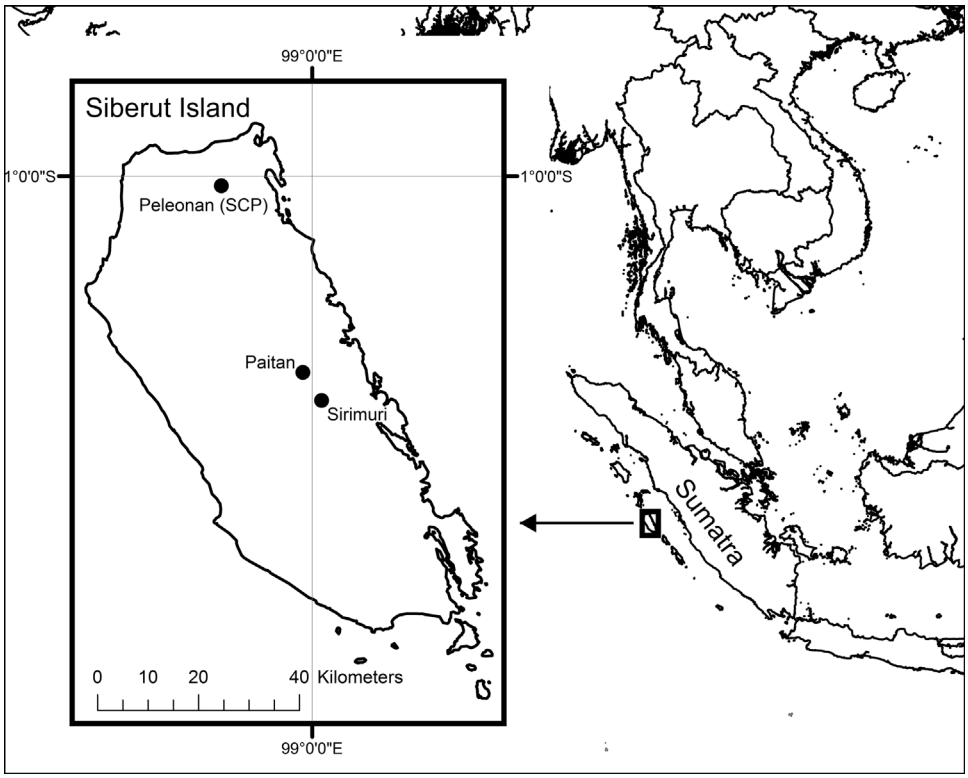

Fig. 1. Location of Siberut Island relative to Southeast Asia. Inset shows the field sites for this (Peleonan (SCP)) and previous studies (Paitan and Sirimuri) of Kloss gibbons.

protected from hunting since 2003, under an agreement with the SCP and the traditional land owners.

Locating Gibbons

We located gibbons by walking along transects and pausing at 200 m intervals for 15 min or more (to listen for vocalizations or canopy movement), by visiting known feeding trees that were fruiting, and by approaching gibbons while they were singing. Kloss gibbon songs can be heard over a kilometer away by humans on the ground and male and female songs are acoustically different [Tenaza, 1976; Whitten, 1982a]. For the first 14 months of the study we listened for male singing from the camp and then approached either the nearest singing male or a male from a focal group. If there was no clearly audible singing, we entered the forest at 0530 to begin searching the radiating transect system and food trees. If not already following gibbons when females sang, we approached the closest group of singing females. In the last 4 months of the study we sat at one of seven listening posts (three in clearings and four on ridges) from 0515 to 1000 and conducted a census. We recorded the number of individual males or groups of females heard in the male and female choruses respectively, individual song duration when we could hear all song components for an individual and total chorus duration (from the beginning of the first audible song to the end of the last). While individuals from different groups sing at the same time, the phrases of their songs are not synchronized. This feature, in combination with the direction and volume of songs (an estimate of distance), enabled us to differentiate between individual males (or groups of females) to census individuals/groups engaged in a chorus. We then approached the closest singing individuals. Like traditional Mentawai hunters, we used the sound of the gibbon song to mask the sound of our approach and paused and remained silent during any pauses in the song. Unlike hunters, we made every effort not to disturb gibbons during singing by keeping our distance and remaining hidden until the singing ended. Over the course of the study period a group of six gibbons (group A) became habituated to our presence and we made progress towards habituation of two more groups (N and B).

Data Collection

For each encounter we noted the date, time, number of gibbons, sex and age class (if known) and activity observed (including their reaction to us). Their monochromatic black pelage makes Kloss

gibbons difficult to differentiate. Adult males were identified by the presence of a scrotum and/or male song. Adult females were identified by elongated nipples (indicating previous suckling). Individuals were also classified as female if they participated in singing the female song; immature females within a group sing with their mother [Dooley et al., 2013]. Age class follows the classification methods of Palombit [1992]. We recorded GPS coordinates when we located gibbons using a Garmin GPSmap® 76Csx handheld GPS unit. We observed gibbons from hiding throughout the study but on 120 of the 164 occasions when we encountered unhabituated gibbons we were detected. We knew when gibbons detected us because one individual would orient and emit alarm notes in our direction which probably alerted nearby gibbons. We defined an "interaction" as seeing gibbons and, in turn, being detected by them.

During "interactions" we noted the distance between us and the gibbons (never less than 10 horizontal meters) and took ad libitum notes on their reaction to us. When gibbons detected us, they reacted with varying degrees of tolerance, which we classified into four categories: 1 = gibbons did not leave the area, 2 = gibbons left after 10 min or more, 3 = gibbons left in under 10 min, and 4 = gibbons fled immediately. When we lost gibbons and did not find them again for at least an hour, we classified the next set of observations as a separate "follow."

Groups A, B, and N consisted of 6, 5, and 7 individuals respectively. If at the beginning of a follow we detected fewer than the total number of individuals for a group we classified this as a subgroup provided we could not detect any other gibbons within a 30 m radius of the gibbons we were observing, nor see or hear any incidental movement in the canopy or gibbon vocalizations that suggested other group members were nearby.

The observation of wild gibbons for this research was approved by The Indonesian Institute of Sciences (LIPI) and by The University of Western Australia Animal Ethics Committee. Research was conducted in accordance with the laws of the Republic of Indonesia and the American Society of Primatologists' (ASP) principles for the ethical treatment of nonhuman primates.

The data presented below are primarily descriptive. We compare the number of individuals sighted between the different song types (pre-dawn male singing, female singing, and post-dawn male singing) in order to examine the advantages of having more or fewer individuals present during each singing condition. Unhabituated Kloss gibbons sometimes responded to our presence with a distraction display which we term "decoy" behavior and describe in more detail below. We compare the number of individuals sighted when a "decoy" response occurred and when no "decoy" response occurred. Data were not normally distributed, so for comparative analysis of the number of individuals sighted during these different conditions we performed Mann–Whitney U tests. Because we have multiple samples of each group in our comparisons, we conducted Kruskal–Wallis tests to determine if there were significant differences among groups (using group ID as a categorical independent variable) for the number of individuals present *within* each condition (pre-dawn male singing, female singing, post-dawn male singing, "decoy" response to humans, no "decoy" response). There was a significant difference among groups for the number of immatures present during interactions where no "decoy" occurred (Kruskal–Wallis: $X^2 = 14.94$, df = 5, $P = 0.011$, $N = 62$); however, groups A, B, and N were not significantly different from each other so only observations of these three groups were pooled for the Mann–Whitney U-test comparing number of immatures present during "decoy" and no "decoy" responses. For all other comparisons there were no significant differences among groups for any of the conditions so observations were pooled for Mann–Whitney U tests.

Spearman's rank correlation was used to examine the relationship of observer-gibbon distance to the graded reaction of gibbons. All statistical analyses were conducted in SPSS version 17.0. GPS points were mapped in ESRI ArcGIS version 10.1. Geospatial Modelling Environment (GME) Version 0.7.2.1 was used to create minimum convex polygons representing maximum home range estimates for groups A, B, and N based on all sightings of these groups (Fig. 2).

RESULTS

Behaviors Minimizing the Risk Associated With Singing

Kloss gibbons sing in same sex choruses where a large portion of an individual's song overlaps temporally with the songs of his/her neighbors. On average, 4.4 males sang during a male chorus (±SD 1.1 males, $N = 18$ choruses) and the mean duration of individual songs was 44.5 min (±SD 14.1 min, $N = 10$ songs). The overlap of songs resulted in an average total chorus duration of 65.8 min (±SD 22.3 min, $N = 21$ choruses). On average, 4.6 groups sang in the female chorus (±SD 1.4 groups, $N = 19$ choruses) and the mean duration of individual songs was 15.4 min (±SD 5 min, $N = 20$ songs). The total duration of female choruses averaged 39 min (±SD 13 min, $N = 19$ choruses) due to groups singing at the same time.

On average, male pre-dawn choruses ended 11.9 min before dawn (±SD 13.1 min, $N = 21$) and members of a group then tended to move away from the singing site (also the sleeping tree) in the low light before dawn. This made it very difficult for us to see and follow gibbons after locating a male singing pre-dawn. All group members are generally present when

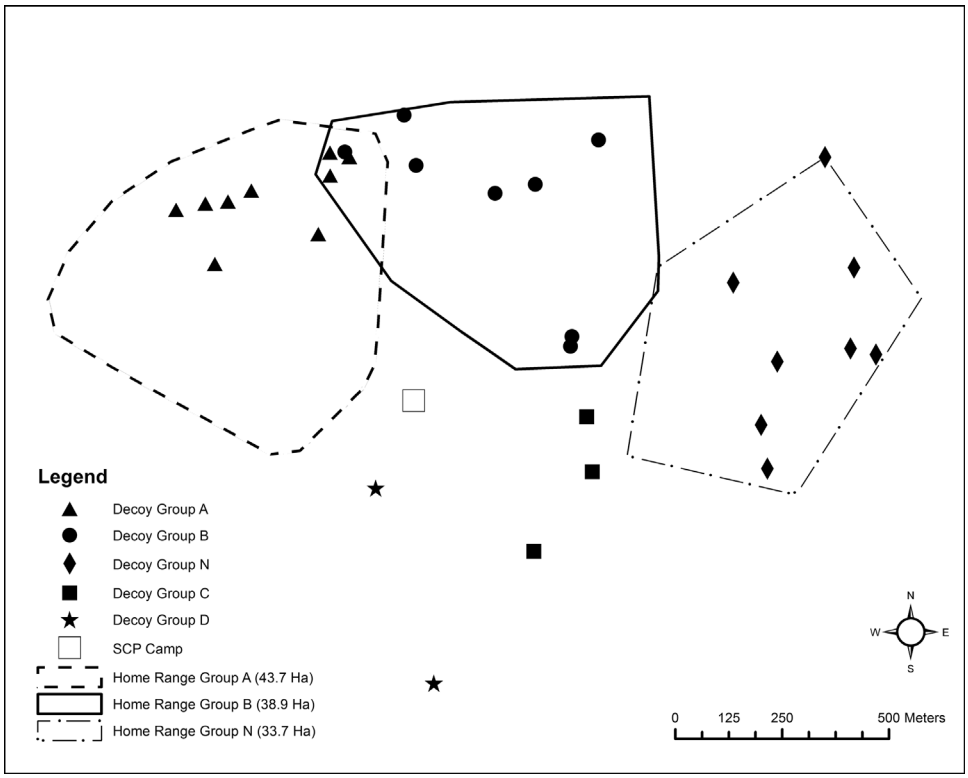

Fig. 2. Locations where "decoy" behavior was observed for each group and the home ranges of groups A, B, and N (minimum convex polygons created from all sightings for each group).

a male sings pre-dawn and when females of a group sing post-dawn; males sing from the sleeping tree and individuals in a group come together in the same tree during female singing. Despite the fact that all group members are generally present, on 7 of the 27 occasions when we approached a male singing during the pre-dawn darkness, we were unable to see any gibbons once it became light. On the 20 mornings when we did see gibbons following a pre-dawn male song, we visually detected fewer individuals ($X = 2.4$ individuals, ±SD 1.4) than during and following a female post-dawn song ($X = 4.2$ individuals, ±SD 1.3, Mann–Whitney U-test: $Z = -4.1$, $P < 0.001$, $N = 58$).

In comparison to pre-dawn singing by males, post-dawn singing by males occurs less often, is less likely to result in a chorus [see Dooley et al., 2013] and is also shorter on average at 31.2 min (±SD 14.4 min, $N = 16$ separate songs). We visually observed males singing after dawn on nine occasions. On seven of the nine occasions when we encountered males singing their solo songs during daylight hours, only part of their group was present and on only three of those occasions were immatures present. There were fewer individuals present when the male sang post-dawn ($X = 2.6$ individuals, ±SD 1.5) than when the females of the group sang in the mid-morning ($X = 4.2$ individuals, ±SD 1.3, Mann–Whitney U-test: $Z = -2.8$, $P = 0.006$, $N = 47$). Once when we observed the male from our focal group singing alone in the late morning, he traveled over 100 m to join the rest of his group after he concluded singing.

Female singing is the most conspicuous Kloss gibbon behavior because it provides an auditory signal during daylight as well as a visual display of shaking branches and rapid movement in the canopy during the climax of the great call. Kloss gibbon females have the lowest daily frequency of singing (0.24 songs each day) of all *Hylobates* females (Table I). While song duration was similar, and even longer than some other species (e.g., *H. moloch* and *H. pileatus*), the overall time spent in diurnal vocal activity for Kloss females was lower (3.7 min of singing each day; Table I).

Crypsis

Groups in the Peleonan consisted of 5.8 individuals on average ($N = 5$ groups, range: 5–7). We observed group fission in the three groups with whom we had the most contact time (A, B, and N). Full groups were present on 50% or fewer separate follows (Table II). When examining only the first observation of a day for focal group A (to control for any effect of gibbons having seen humans earlier in the day), the entire group was present on only 46% of first daily observations ($N = 35$ days). The juvenile

TABLE I. Song Durations and Daily Frequencies for *Hylobates klossii* Females in Comparison to Females of Other *Hylobates* Species

	Females			
Species	Average duration (minutes)	Frequency (each day)	Mean, minutes (each day)	Source
Hylobates klossii	15.4	0.24	3.7	This study
	20	0.18–0.27	3.6–5.4	Paitan River, Siberut Island, Indonesia [Whitten, 1982a]
	21	0.22	4.6	Sirimuri River, Siberut Island, Indonesia [Tenaza, 1976]
H. moloch	7	1.2	8.4	Dieng mountains Central Java, Indonesia [Geissmann & Nijman, 2006]
	9.5	0.6	5.7	Ujung Kulon-Gunung Honje Nature reserve, West Java, Indonesia [Kappeler, 1984]
H. agilis	17	1.9	32.3	Sungai Dal and Ulu Muda Forest Reserve, Gunung Bubu Forest Reserve, Malaysia [Gittins, 1984]
	—	0.62	—	Sabangau Catchment, Central Kalimantan [Buckley et al., 2006]
H. pileatus	11–13.8	—	—	Chipat, Cambodia and Botum Sakor, Cambodia [Traeholt et al., 2006]
	—	0.43	—	Khao Soi Dao Wildlife Sanctuary, Thailand
			4.7–5.9[a]	[Brockelman & Srikosamatara, 1993]
H. muelleri	15.63	1.03	16.1	Kutai game reserve, Kalimantan, Indonesia [Mitani, 1985]
H. lar	11.5	1.3	15	Khao Yai National Park, Thailand [Raemaekers et al., 1984]
	24.4	0.51	12.4	Ulu Gombak Field Studies Centre, Malaysia [Chivers, 1974]

— Data deficient.
[a]Values calculated from values for duration and daily frequency of songs reported by Brockelman & Srikosamatara [1993] and Traeholt et al. [2006].

and adolescent from group A were always accompanied by either the adult female, adult male or subadult female and there was no pattern of sub-group membership that would indicate that fission was due to peripheralization of one or more individuals. Group A engaged in foraging just as often when they were a partial group as when all group members were present (83% of 58 follows of full group, 82% of 103 follows of partial group). We did not observe any highly-aggressive behavior during follows of either full or partial groups that would indicate strong competition for food.

We rarely observed gibbons engaging in non-vocal social behavior. Of 214 observation days (328 hr of visual contact), social grooming was only observed on 4 occasions and play on only six occasions. All instances of play were brief and occurred during periods of foraging. All four observations of grooming included two or more individuals sitting close together on a large branch, alternating between grooming and resting. We cannot calculate the average duration of these grooming bouts, because three of the four observations were of unhabituated gibbons who became aware of our presence and fled. We only observed social grooming once in the habituated focal group; it was a prolonged bout occurring within a sleeping tree at 1700 hours and consisted of two grooming dyads.

TABLE II. Percentage of Separate Follows of *H. klossii* Groups When Whole or Partial Group Was Present

Group	% follows full group	% follows partial group	Total number of follows
A	36	64	161
B	38	62	58
N	50	50	34

Response to Humans

Kloss gibbons responded to our presence by emitting alarm notes (which sometimes led to a full alarm call) leaving the area quickly and sometimes by engaging in a distraction display described below. Only humans elicited an alarm call from the gibbons. In accordance with Tenaza & Tilson's [1977] description of alarm calling in Kloss gibbons, alarm calls by gibbons in the Peleonan also consisted of sirening and

alarm trills. We did not see large reticulated pythons capable of capturing immature or adult gibbons during our time at the site and we never observed Kloss gibbons mobbing snakes. We rarely saw raptors in the air and never observed any gibbons responding to them. Kloss gibbons sometimes encountered other primates and foraging pigs but we never observed them alarm call, flee or engage in a distraction display in response to these animals.

This study included 120 interactions with unhabituated gibbons who detected us; in 72% of these interactions gibbons fled immediately. The closer we were to unhabituated and partially habituated gibbons when they detected us, the more likely they were to flee immediately rather than stay in the area for 10 min or more (Spearman's $\rho = 0.328$, $P < 0.001$, $N = 228$). The mean distance between humans and gibbons during interactions when gibbons fled was 34.5 m (±SD 14 m).

On 30 occasions we observed a behavior, not previously described for any gibbon species, which we term "decoy" behavior. Upon detecting humans, gibbons gave alarm notes that sometimes led to a full alarm call. This alerted other group members who also vocalized and, in the case of a full alarm call, often alerted neighboring groups who then alarm called in response. Subsequently, one adult individual would approach us and, on a lower branch in full view, perform a display of exaggerated shifting of body weight from side-to-side while observing us and emitting loud alarm notes. During this display, other group members split into sub-groups and dispersed covertly in various directions. Lastly, the distracting or 'decoy' individual also would flee. The "decoy" individual was always an adult male or a sub-adult; adult females with infants never acted as the "decoy" individual. When group members fled in different directions, young immatures were always accompanied by older/larger individuals. We observed this "decoy" behavior in five groups over the course of the study (Fig. 2), and it accounted for 31% of 96 interactions with unhabituated gibbons in groups (more than 1 individual present). During the majority of "decoy" reactions, all gibbons left the area within 5 min of detecting us. A "decoy" reaction was more likely to occur when there were more individuals and more adult sized individuals present (Table III).

DISCUSSION

The Kloss gibbon (*H. klossii*) is endemic to the Mentawai Islands in Indonesia and has been subject to human predation for over 2000 years in the absence of other significant predators [Tenaza, 1976; Tenaza & Tilson, 1977, 1985; Tenaza & Mitchell, 1985]. Kloss gibbons offer a unique opportunity to examine the human avoidance strategies of a gibbon species whose evolved behavioral defenses are not constrained by responses to other predators and thus may be more specialized to human predation. The behaviors that we suggest lower the risk of human predation include: chorusing, singing less during daylight hours, males singing away from group members during post-dawn male songs and being present but silent when females of the group sing, group fissioning during daily activity, spending less time engaged in conspicuous behaviors such as play and social grooming and, finally, responding to humans by fleeing immediately, alarm calling and/or engaging in a "decoy" display.

Behaviors Minimizing the Risk Associated With Singing

In all populations studied so far, Kloss gibbons have been observed to sing their solo songs in chorus with same sex neighbors [Tenaza, 1976; Whitten, 1982a]. By singing at the same time as neighbors, individuals can lower their individual risk of predation via the dilution effect [Tenaza, 1976]. Chorusing presents auditory signals from multiple and

TABLE III. Number of Individuals, Immatures, and Adult Gibbons Relative to the Presence/Absence of "Decoy" Responses to Human Presence

						Mann–Whitney *U*-test	
Decoy	*N*	Min.	Max.	*X*	SD	*Z*	*P*
Number of individuals							
Yes	30	3	6	4.7	0.99	−3.755	<0.001
No	66	2	6	3.8	1.22		
Number of adults[a]							
Yes	30	1	3	2.0	0.54	−2.257	0.024
No	64	0	3	1.7	0.65		
Number of immatures[b]							
Yes	25	1	4	2.1	0.83	−2.194	0.028
No	53	0	3	1.6	0.84		

[a]Total number of observations varies because, for some observations, we were unable to determine the age class of fleeing individuals.
[b]Mann–Whitney *U*-test conducted on groups A, B, and N only because there were no significant differences among these groups for number of immatures present within each condition.

diverging sources to hunters localizing prey by song. This makes it more difficult for hunters to discriminate and orient to a singer's location than if there was only one individual singing. Larger aggregations of individuals in some animal species can lead to a "confusion effect" on predators, limiting their ability to home in on one individual [Landeau & Terborgh, 1986; Tuttle & Ryan, 1982]. Chorusing in Kloss gibbons may cause an auditory "confusion effect." Alternatively, chorusing may occur because individuals are stimulated to sing by hearing their neighbors singing, but the overlap of songs with neighbors comes at the cost of signal clarity to conspecifics. In fact, *H. moloch* females avoid singing at the same time as neighbors presumably for this reason [Geissmann & Nijman, 2006]. Perhaps *H. klossii* males occasionally risk singing post-dawn because chorusing is less likely to occur at this time.

The pre-dawn songs of male Kloss gibbons provide an auditory signal to hunters. By singing their regular solo songs completely in the dark before dawn, Kloss gibbon males reduce the visual signal for hunters making it harder for them to pursue and capture gibbons. Weather conditions in the early hours of the morning provide the perfect environment for the propagation of sound and this may explain why males sing pre-dawn [Whitten, 1982a]. However, gibbons in the Peleonan left pre-dawn singing locations rapidly before first light, and Kloss gibbon groups in the Paitan River population travel furthest to the first feeding tree on days when resident males sing pre-dawn [Whitten, 1982a]. This limits visual detection by hunters and suggests that male pre-dawn singing and the behavior accompanying it is, in part, due to avoiding human predation and not just a response to optimal weather conditions.

In contrast to male pre-dawn singing, female singing occurs during daylight and provides hunters with both an auditory and visual signal that may be detected from a long distance [Tenaza, 1976]. Female singing in all gibbons, whether in duet or solo, includes a visual display of branch-shaking and acrobatic brachiation [Geissmann, 2000; Gittins, 1984; Haimoff, 1984]. Solo singing by females is the most conspicuous behavior displayed by Kloss gibbons and therefore they should limit the time they spend engaged in this behavior under the threat of predation. Kloss gibbon females in all three populations studied so far, sing less often than females of other species (Table II). Perhaps without the vocal stimulation of a mate (as in duetting species) Kloss females are not enticed to sing as often. If this is the case, female *H. moloch* (the other species in which duetting is absent) should also have a low daily singing frequency, but, they appear to sing as often as females from duetting species (Table II). Alternatively, a reduction in the time spent engaging in this conspicuous behavior may be a response to long-term human predation.

The absence of the duet in Kloss gibbons reduces the risk of predation by humans. During female Kloss gibbon songs, immature females join the adult female in singing and displaying; as a result, all females in a group are vulnerable during female song. In duetting gibbon species, however, males not only sing during duets, but may also engage in the visual display during the great call of the females [Geissmann, 2000; Gittins, 1984; Haimoff, 1984]. However, male Kloss gibbons are present during the female song but do not sing and we never observed males engaging in the visual display. Given that duetting behavior is likely to be ancestral [Geissmann, 2002], why do male Kloss gibbons remain with their mates during the female song, but not sing or display with them? There are two advantages of males being present but remaining silent: firstly, males can remain vigilant throughout the song and thus offer the advantage of early detection of hunters. Secondly, there are periods of silence between the female great call phrases, because the male component is missing and during these silent periods, gibbons of either sex may listen for the approach of hunters. Perhaps the loss of the duet in Kloss gibbons is a response to a long period of human predation pressure, where the duet was the most conspicuous and the riskiest behavior in all phases of predation.

Occasionally males also sing during daylight hours. Unlike female songs, male songs do not contain a visual display; thus, while the auditory signal to a hunter is strong, the visual signal is not. Males sit relatively still while singing and can remain vigilant and detect approaching predators [Tenaza, 1976]. While males of other gibbon species sing solo songs within the vicinity of other family members [Mitani, 1988], we observed Kloss gibbon males singing away from other group members during post-dawn songs. Tenaza [1976] also observed males in the Sirimuri River population singing away from family members during post-dawn solos. We suggest that this reduces the risk to their mate and offspring.

Crypsis

Many primates employ a cryptic strategy to avoid detection by predators [Colquhoun, 2006; Fichtel, 2012; Isbell, 1994; Miller & Treves, 2007]. We suggest that group fission and low levels of social behavior observed in Kloss gibbon groups in the Peleonan is part of a cryptic behavioral strategy to avoid detection by hunters. Kloss gibbons spend less time engaged in social interactions such as grooming or play than other gibbon species [Fuentes, 2000], making them more cryptic during daily activity. We rarely saw play interactions, even though the three most observed groups each included a juvenile and adolescent, age classes for which play is common [Bartlett, 2003; Burns et al., 2011; Reichard & Sommer, 1997]. By spending little time grooming

and playing, Kloss gibbons reduce visual and aural signals because canopy displacement is minimized (playing) and individuals are not clustered together (grooming) thereby making them more cryptic during daily activity.

In other gibbon species and the two Kloss gibbon populations previously studied, family members are usually within visual contact throughout daily foraging and traveling [Bartlett, 2009; Tenaza, 1975; Tilson, 1980; Whitten, 1982b], but Kloss gibbons in the Peleonan frequently forage and travel in sub-groups. In the Peleonan forest, average group size is close to six individuals, whereas in other populations of Kloss gibbons, average group size is fewer than four individuals [Tilson, 1981; Whitten, 1982b]. Larger groups of animals suffer an increased risk of detection by predators; however, this cost is usually outweighed by the advantage of decreased individual risk of predation due to both dilution [Anderson, 1986; Hamilton, 1971; Wrona & Dixon, 1991] and increased vigilance, leading to earlier detection of, and response to, predators [van Schaik et al., 1983]. The advantages of living in larger groups are constrained by living in nuclear family groups [Brockelman, 2009]. Larger gibbon groups are unlikely to be more vigilant because of the high proportion of immatures, and the advantages of dilution effects would not outweigh the increased cost of being detected by predators because the loss of a closely related group member to predation lowers an individual's inclusive fitness. By fissioning during daily activity, Kloss gibbons in the Peleonan reduce the risk of detection by human hunters.

It might be argued that resource competition and energy constraints result in fission and the low levels of play and grooming exhibited by these gibbons. Living in large groups can increase competition for food resources such that when predation pressure is lower, foraging group size may also be lower [Link & Di Fiore, 2013]. Larger bodied primates generally have a lower risk of predation and they are therefore able to fission into smaller groups during foraging to reduce resource competition [Bettridge et al., 2010; Isbell, 1994; Lehmann et al., 2007; Link & Di Fiore, 2013]. We cannot rule out energy constraints as the cause of group fission and low levels of play and grooming in Kloss gibbon groups without detailed information on feeding patch sizes and the energetic quality of foods eaten. However, we suggest that fission of gibbon groups is part of a cryptic strategy and not a response to foraging pressure in the absence of high predation risk for several reasons. It is unlikely that the "larger" body size of Kloss gibbons [approximately 5.8 kg, Tenaza & Hamilton, 1971] reduces their risk of predation by humans because hunters preferentially choose larger prey animals, hunt cooperatively and are able to capture prey with the use of projectile weapons [Isbell, 1994; Kumpel et al., 2008; Miller & Treves, 2007; Peres, 1990; Zapata-Ríos et al., 2009]. Furthermore, resource competition is unlikely to be the selective pressure driving these groups to fission because gibbons foraged as a whole group just as often as they did in sub-groups. Group and home range sizes (five to seven individuals on 33.7–43.7 ha, Fig. 2) seen in the Peleonan are also within the range seen in other gibbon populations for which there are no descriptions of group fission [Malone & Fuentes, 2009] nor any evidence of higher food availability than in the Peleonan. Additionally, if groups were experiencing foraging pressure, we might expect to see intra-group aggression and peripheralization of sub-adults rather than group fission, because adult-sized offspring would be competitors for food; however, intra-group aggression was rare and the sub-adult female from Group A was often seen foraging with the adolescent female and adult male. For these reasons we hypothesize that the group-fission behavior of Kloss gibbons described here is related to crypticity and reducing the risk of detection by humans.

Response to Humans

Following the detection of predators, gibbons of other species may alarm call and increase the distance between themselves and the predator [Clarke et al., 2012; Uhde & Sommer, 2002]. The similar responses of unhabituated Kloss gibbons to our presence suggests that they regarded us as predators. The fact that we only observed Kloss gibbons alarm calling in response to humans and never in response to interspecific food competitors or non-threatening terrestrial animals (e.g., pigs) also suggests that Kloss gibbons recognize humans as a threat. This is supported by our observations of Kloss gibbons rapidly fleeing an area following the detection of humans.

The "decoy" behavior we observed in the Peleonan population has not been described previously for *H. klossii* or other gibbon species. This behavior appears to lower the success of hunters in both pursuit and capture of Kloss gibbons. The "decoy" reaction to predators demonstrated by Kloss gibbons, where one individual acts as a distractor to allow the escape of more vulnerable (and highly related) groups members, draws parallels to the nest distraction behaviors of some bird species [Bures & Pavel, 2003; Montgomerie & Weatherhead, 1988]. In gibbons, acting as a distractor to reduce the risk of predation to more vulnerable family members will increase an individual's fitness, particularly if that individual is more adept at avoiding being captured than other group members. This accords with our observations that only adult males and sub-adults acted as "decoys" during our encounters with unhabituated gibbons.

Kloss gibbons differ from other gibbon species in that humans are their primary predator [Tenaza &

Tilson, 1985]. We propose that many behavioral differences observed between Kloss gibbons and other gibbon species may be attributed to this long history of human predation pressure. Specifically, chorusing, the loss of the male part of the duet, and a reduction in the time spent singing during daylight hours all reduce the risk associated with the most conspicuous hylobatid behavior. Lower levels of non-vocal social activity and fission during daily activity in combination with monochromatic black pelage serve to lower risks of detection at closer distance. Upon detection, a coordinated decoy response to humans serves to lower the risk of capture by human hunters. While one behavioral difference alone may not be attributed to an evolved response to human predation, as a whole, the suite of behaviors exhibited by Kloss gibbons suggests an evolved response to a long history of human predation pressure.

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